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A NEW LOOK AT SPHAGNUM SECT. ACUTIFOLIA IN SOUTH AMERICA

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The members of *Sphagnum* sect. *Acutifolia* are difficult to deal with, because so many of them look alike and are perforce defined by microscopic features difficult to describe, troublesome to observe, and subject to varied interpretations. Taxonomic decisions at the species level are highly subjective, and agreements on species limits are by no means unanimous, especially in this section of the genus. Certainly, mindless acceptance of species based on characters staunchly defended by some and airily dismissed by others is not desirable. And it scarcely helps to lump variants to the extent that species lose definition. The South American species of the *Acutifolia* need to be redefined because of excessive lumping.

As I have stated elsewhere, I have the greatest respect for A. LeRoy Andrews' work, yet the more I try to understand the difficult taxonomy of *Sphagnum* the more I find his concept of species unacceptable. In his 1947 account of the South American *Acutifolia*, he recognized eight species and relegated many others to the netherworld of synonymy. He was patently conservative in taxonomic judgment, yet he had taken the opportunity to study the types in the Warnstorf Herbarium in Berlin, and those all-important specimens are, in many cases, no longer in existence. Not having seen the types of many of the *Acutifolia*, I can scarcely rail out against the master. But Andrews' abbreviated definitions of species can be compared and contrasted with Warnstorf's detailed and generally accurate ones in the *Sphagnologia Universalis* of 1911. It is on that basis and on the basis of my own observations that I present the following inventory of the South American *Acutifolia* that Andrews brought under scrutiny in 1947. I make no reference here to the numerous other *Acutifolia* that I have described from South America in recent time.

1. Sphagnum sparsum Hampe (figs. 1–10) is a small moss of modest appearance growing in dense, pink or pink-tinged cushions. It has the general aspect of *S. capillifolium* (Ehrh.) Hedw., not that of *S. warnstorfii* Russ., as Warnstorf (1911) said. Andrews (1947) correctly commented on the small, ringed pores commonly grouped in threes at adjacent corners of hyaline cells of branch leaves, on their outer surfaces, and also on the decided convexity of those cells. Other diagnostic features include the porose epidermal cells of the stems and the hyalocysts of stem leaves consistently divided and having membrane pleats and only weakly developed fibrils. I have not seen the type collection (from the vicinity of Rio de Janeiro, *Glaziou 3535*), but there is no question in my mind that Hampe described a plant comforming to Warnstorf's concept and my own. In the original description (1870), Hampe gave notice of stem leaf hyalocysts as "evidenter striatis, inanibus; in supe-

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FIGS. 1–7. Reasonably typical expressions of *Sphagnum sparsum* as represented in Mexico (and elsewhere in a broad range). 1. Branch leaves, ×23. 2. Upper cells of branch leaf, outer surface, ×358. 3. Portion of branch leaf in section, ×358. 4. Epidermal cells of stem, ×358. 5. Stem leaves, ×23. 6. Upper cells of stem leaf, outer surface, ×358. 7. Upper cells of stem leaf, inner surface, ×358.

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FIGS. 8-10. Variant of Sphagnum sparsum drawn from an apparent topotype "Colombia, San Cristóbal, Bro. Ariste-Joseph, Jan. 1905" (NY). 8. Upper cells of branch leaf, outer surface, ×430. 9. Upper cells of branch leaf, inner surface, ×430. 10. Upper cells of stem leaf, outer surface, ×430.

riore parte folii cellulis brevioribus subrhombeis, fibris tenuissimus." Judging from his determinations, I believe that Andrews held a similar concept, although I question whether some of the names that he placed in synonymy belong in S. sparsum. My only knowledge of S. pseudocapillifolium C. M. & Warnst., S. itatiaiae C. M. & Warnst., and S. roseum Warnst. is derived from Warnstorf's detailed descriptions. Although those species seem to have small, ringed pores on the outer surfaces of branch leaves, they appear to have no pores in the epidermal cells of their stems. I agree, however, that S. apollinairei Par. & Warnst. is an expectable variant from the S. sparsum norm, with hyaline cells of stem leaves more elongate, with well-formed fibrils, and numerous round to oblong membrane gaps. Such plants have been seen from several parts of the range of S. sparsum. I have not seen an identifiable type of S. apollinairei, but I have examined two specimens collected near Bogotá by Bro. Ariste-Joseph in January 1905 (perhaps the same place and date as the type), also named S. apollinairei n. sp. (NY). That material was used in preparing figures 8-10 to show contrast with normally developed material from Mexico. Sphagnum sparsum is one of the most commonly collected species of the genus in the mountains of northern South America. I have seen many specimens from Colombia, Venezuela, Ecuador, Bolivia, and Peru, as well as Mexico, Guatemala, and Costa Rica. The species occurs at elevations of 2250–3900 m, probably most commonly above tree line, often in páramos, but in Mexico, at least, it grows in moist, montane forests. The distributional range and preferred habitat are such that a Brazilian type locality, in the vicinity of Rio de Janeiro, seems phytogeographically anomalous. I have seen no specimens from Brazil.

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2. Sphagnum oxyphyllum Warnst. (figs. 11–17) is a beautiful moss of moderate size, varying from pink to a dark wine-red. The branch leaves are erect and nicely five-ranked when moist. On drying they become slenderly concave-acuminate, loosely curved-spreading, and often secund. The stem leaves show some variability in shape and in the strength of the border. They are normally sharply cuspidate-pointed, but the point varies from gradually acute to abruptly concave-pointed. (It is the sharpness of the stem leaves to which the specific epithet applies.) Most commonly the border is only slightly broadened at the base of the leaves, but it can be abruptly expanded below.

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The type collection was cited as "Brasilien, Tubarão, am Rande der Serra Geral von E. Ule 1890 gesammelt" (Warnstorf 1890). In a later publication (1911), Warnstorf cited collections as "Südbrasilianische Province: St. Catharina, am Rande der Serra Oratorio (Ule n. 651); Serra Geral (Ule n. 1102); Abhänge der Serra do Itatiaia, 2000–2300 m. u. M. (Ule n. 1744, 1903)." By locality designation it thus appears that *Ule 1102* is the type. At the Berlin Museum is a specimen from Warnstorf's herbarium filed as *S. oxyphyllum* and marked Typus. It is labeled "*Sphagnum subaciphyllum* C. M. Sta. Catharina, Serra Geral, Ule n. 1102." (*Sphagnum subaciphyllum* is an unpublished name.) The specimen conforms in every way to Warnstorf's descriptions (1890, 1911) and Andrews comments (1947) based in part on specimens he saw in Warnstorf's herbarium. Georg Roth's unpublished drawings in the herbarium of the University of Michigan, presumably made from authentic material, are not particularly informative; they show concave-pointed stem leaves, though not as emphatically as Warnstorf illustrated them. Ule's *Bryotheca Brasilensis* 240, from the Serra do Itatiaia (NY), distributed as *S. oxyphyllum*

Warnst. n. sp., was collected in 1894, four years after the species was described. But it certainly conforms well to the type specimen (*Ule 1102*) and so does the specimen that Andrews referred to as a good one (*Tate 482*, Venezuela, NY).

A Brazilian specimen labeled *S. hymenophyllophilum* C. M. *ms.* from "Sta. Catharina, Serra Geral, *Ule 27*" (US) clearly belongs to *S. oxyphyllum*. It is the only fruiting specimen seen, but the capsules contain, intead of *Sphagnum* spores, those of the fungus *Tilletia sphagni*.

Sphagnum oxyphyllum var. nanum C. M. & Warnst. ex Warnst. (1897) was characterized as having terete-foliate branches and sharply apiculate stem leaves. Warnstorf, in a later publication (1911), gave it specific status as *S. parvulum* Warnst., and Andrews (1947) referred the latter to the synonymy of *S. capillifolium* (Ehrh.) Hedw., actually under the name *S. capillaceum* (Weiss) Schrank. The description provided by Warnstorf scarcely suggests a closeness to *S. oxyphyllum*, yet I am hesitant to accept Andrews' disposition of the species as his concept of *S. capillifolium* was very broad and, furthermore, I have seen no South American

material that I would refer to that species.

Andrews (1947) included *S. weberbaueri* Warnst. in the synonymy of *S. oxyphyllum.* From Warnstorf's description and illustrations (1907, 1911), I am tempted to accept Andrews' disposition of the species. Yet some features do not accord with *S. oxyphyllum.* As Warnstorf described *S. weberbaueri*, the plants are grayish green; the stem cortex is 2-layered and lacks pores; the hyaline cells of the stem leaves are not much divided and have numerous gaps on the inner surface; and the branch leaves, though 5-ranked and curved, are erect-spreading. It may be noted that Warnstorf (1907) considered *S. weberbaueri* closest in its characters to *S. purpuratum* C. M. and later (1911) to *S. itatiaiae* C. M. & Warnst. Andrews considered *S. itatiaiae* a synonym of *S. sparsum* and placed *S. purpuratum* in synonymy

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FIGS. 11–17. Sphagnum oxyphyllum (drawn from Venezuelan specimen, Tate 482, NY). 11. Branch leaves, $\times 23$. 12. Portion of branch leaf in section, $\times 358$. 13. Upper cells of branch leaf, outer surface, $\times 358$. 14. Epidermal cells of stem, $\times 23$. 15. Portion of stem in section, $\times 358$. 16. Stem leaves, $\times 23$. 17. Upper cells of stem, outer surface, $\times 358$.

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with S. tenerum Sull. & Lesq., but the isophylly which above all else characterized S. tenerum is not featured in the description of S. purpuratum and certainly not in the description of S. weberbaueri.

The type collection of *S. weberbaueri* was made in Peru, at 2600 m altitude. I have seen no specimens of *S. oxyphyllum* from Peru, and I do not know whether its occurrence there is phytogeographically reasonable or not. I have seen numerous specimens of *S. oxyphyllum* from southern and Amazonian regions of Brazil, as well as British Guiana, Venezuela, and Colombia, over an altitudinal range of 430 to 2700 m. The plants were found in moist forests and meadows on wet rocks and

banks of soil near streams and waterfalls.

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3. Sphagnum laceratum C. M. & Warnst. ex Warnst. was reluctantly retained by Andrews (1947), although he thought it might be only an aberrant expression of *S. oxyphyllum*. Judging from its description and from Andrews' comments, this species of southern Brazil has the aspect of *S. oxyphyllum* but lacks pores in the stem epidermis and has stem leaves somewhat fringed at the apex and (sometimes) split down the middle, with hyaline cells many-times divided and considerably resorbed on both surfaces. I scarcely see how plants with those characteristics can be considered merely aberrant from *S. oxyphyllum*.

4. Sphagnum meridense (Hampe) C. M. is common in the Cordilleras from Mexico southward and also in the West Indies. It is a beautiful moss, tall, stately, commonly suffused with delicate shades of pink. Andrews (1913, 1947) allowed it a remarkable variability which it loses when it is purged of Sphagnum limbatum Mitt. as a synonym. Interesting features of S. meridense include the equal exposure of green cells of branch leaves and the pore structure on both surfaces of branch leaf hyalocysts. There are only a few elliptic, ringed commissural pores on the outer surface, and toward the leaf tips they are small and mingled with a few minute, round, median pores. On the inner surface are numerous large, round, unringed pores. The hyaline cells of stem leaves generally lack fibrils and gaps, but sometimes show 1-5 irregularly rounded commissural gaps on the inner surface. Andrews (1913) placed in the synonymy of Sphagnum meridense the following: S. antillarum Besch., S. platycladum C.M., S. lesueuri Warnst., S. costaricense Warnst., and S. tonduzii Warnst. I have seen a portion of the type of S. costaricense at US and agree that it belongs here. A portion of the type of S. tonduzii at US belongs in S. limbatum Mitt., a species that Andrews did not distinguish from S. meridense. Judging from Warnstorf's comments concerning S. limbatum and the var. antillarum (Besch.) Warnst. (1911, p. 112), it appears that S. antillarum Besch. and S. lesueuri also belong to S. limbatum rather than S. meridense. Warnstorf gave

no characters that I can use to differentiate the variety from S. limbatum.

The relationship of *S. antillarum* Schimp. ex Warnst. 1891, nom. illeg., of Trinidad, is quite different. Andrews (1941) gave it as a synonym of *S. palustre* L., but Eddy (1977) put it in synonymy with *S. perichaetiale* Hampe. Eddy's disposition of the species is phytogeographically more plausible.

Sphagnum meridense is unlike other members of the Acutifolia in branch leaf sections and in porosity of branch leaf hyalocysts, whereas S. limbatum is thoroughly typical of that section. Because of the red coloration, known in the genus only in the sections Sphagnum and Acutifolia, and the overall appearance of S. meridense, I am content to leave it in the Acutifolia. It is interesting to note, however, that Warnstorf put it into the same section as S. aongstroemii C. Hartm.

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5. Sphagnum limbatum Mitt., when well developed, looks much like *S. meri*dense. However, it comes close to the norm for the section Acutifolia in having green cells of branch leaves exclusively or more broadly exposed on the inner surface and in having numerous large, elliptic, ringed pores at the commissures on the outer surface of hyaline cells. On the inner surface of branch leaf hyalocysts are only a few round, unringed pores, quite inconspicuous in comparison with those of *S. meridense*. The stem leaves have a great many commissural pores on the outer surface of hyaline cells and often rounded commissural gaps resembling pores on the inner surface.

Because of its stem leaves with an abundance of commissural pores on the outer surfaces of hyaline cells, *S. limbatum* can be confused with *S. tenerum* Sull. & Lesq. However, the epidermal cells of the stem are consistently porose in *S. limbatum* and not porose in *S. tenerum*. (In *S. meridense*, some or most of the stem epidermal cells are porose.) *Sphagnum tonduzii* Warnst. fits into synonymy with *S. limbatum*. Warnstorf recognized it as unique because of the fasciation of few to many green cells at the base of stem leaves. His illustration (1911, p. 16, fig. 51) shows a sizable group of cells that failed to differentiate into the usual pattern of hyaline cells enmeshed in green cells. The portion of the type at US (Costa Rica, Cuesta de Tarrazú, *Tonduz,* Feb 25, 1893) shows no such undifferentiated cells, and it appears that Warnstorf's illustration, interesting as it is, represents an anomaly, a teratology of no taxonomic significance. Warnstorf's description is good, but the hyaline cells of stem leaves have on their outer surfaces many ringed, elliptic commissural pores rather than almost no pores, as he said.

Sphagnum limbatum occurs in a broad range in the uplands of Mexico, Guatemala, Costa Rica, northern South America, and the West Indies.

6. Sphagnum tenerum Sull. & Lesq. is a species of the Atlantic and Gulf Coastal Plains of North America difficult to separate from isophyllous expressions of S. capillifolium (Ehrh.) Hedw. I have seen a few specimens from South America (found at altitudes of 1800-2460 m): Southern Brazil, Minas Gerais, Schiffner 297 (F); Colombia, dep. del Valle, Cuatrecasas 20273B (US); Venezuela, Est. Bolívar, Stevermark et al. 10926 (US, MICH); Ecuador, prov. Loja, Luteyn 8049 (NY, MICH), prov. Morona-Santiago, Steere 27814 (NY, MICH). Andrews, after long hesitation (1947), decided to include S. tenerum in the flora of Brazil on the basis of five species that he placed in synonymy. However, according to Warnstorf (1911), S. purpuratum C. M., S. mosenii Warnst., S. aracense Warnst., and S. usteri var. versicolor Warnst. lack pores in the epidermal cells of the stems (as does S. tenerum), but he did not describe them as isophyllous. Only S. campicolum C. M. ex Warnst. is isophyllous and therefore seems likely to be a synonym of S. tenerum. My definition of S. tenerum (and also Warnstorf's) differs from Andrews'. He differentiated the species from S. capillifolium by its robust growth, thick branches with rather large, imbricate leaves having empty cells strongly convex at back "so that their pores tend to be seen more or less in profile, giving them a very narrow elongated appearance." I consider the relatively short and thick branches of the capitulum characteristic but do not think of the plants as robust or the branch leaves as large except perhaps in comparison with S. capillifolium. I do not see the branch leaf hyalocysts as bulging-convex in any distinctive and recognizable way. For me, the essential feature of the species has to do with isophylly. The stem leaves some-

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what resemble branch leaves in shape and structure, being relatively long, narrow, and concave-pointed and having hyaline cells fibrillose and not often divided, with an abundance of ringed, elliptic commissural pores on their outer surfaces. (The epidermal cells of the stem are lacking in pores in contrast to those of *S. limbatum*, which is similarly isophyllous.)

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7. Sphagnum fimbriatum Hook. & Wils., wide-ranging in the Northern Hemisphere, has been collected many times in southern Chile, Patagonia, and the Falklands (and reportedly in Tierra del Fuego), as well as the Transvaal. The type is, in fact, antipodal in origin. Its wide disjunction north and south is indeed remarkable.

8. Sphagnum capillifolium (Ehrh.) Hedw. is so common and so wide-ranging in the Northern Hemisphere that it may well be expected to show disjunct occurrences in South America, yet I have seen no specimens to support Andrews' decision to include the species, as *S. capillaceum* (Weiss) Schrank, in that flora. I define that species in its narrowest sense as having concave-pointed stem leaves with hyaline cells often divided, fibrillose throughout, and usually showing on the outer surfaces of some few hyaline cells a rounded membrane gap. Because of the generalized nature of the species and its lack of definition, I am reluctant to express opinions on the numerous species Andrews relegated to synonymy: *S. rigidum* Hampe & Lor., *S. aciphyllum* C. M., *S. brunnescens* Warnst., *S. diblastum* C. M., *S. densum* C. M. & Warnst., *S. versicolor* Warnst., *S. parvulum* Warnst. (also known as *S. nanum* C. M.), and *S. usteri* var. *viride* Warnst. But the record is such that I would guess that Andrews carried lumping too far!

9. Sphagnum subnitens Russ. & Warnst. ex Warnst. was recorded from South America ("Chile, Patagonien") by Warnstorf (1911), as *S. plumulosum* Röll and also by Andrews (1947), who synonymized *S. mandonii* Warnst. of the Northern Hemisphere. Unfortunately, the species is difficult to recognize either by aspect or by microscopic features and, in any case, the concept which those authors held is unacceptably broad. I recognize *S. subfulvum* Sjörs and *S. flavicomans* (Card.) Warnst. as reasonably distinct segregates from their species concept. Because it is not at all common in the Northern Hemisphere, it is not the kind of species one would expect as a disjunct in South America.

10. Sphagnum molle Sull. may be mentioned here for the sake of completeness. It was not included in the South American flora by Andrews, but Maass (1966) reported a var. *cochabambae* Maass, nom. nud., based on a 1908 collection from Bolivia by Herzog (represented in herb. Jena and Munich). According to Maass, the plants show a resorption furrow in some branch leaf sections, but the chlorophyll cells are atypical, being narrowly triangular to nearly fusiform, with the outer wall thickened.

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